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Genetic Consequences of Group Living in Mongolian Gerbils

YANNI WANG, WEI LIU, G. M. WANG, WENQIN ZHONG, AND XINRONG WAN

From the State Key Laboratory of Integrated Management of Pest Insects and Rodents, Institute of Zoology, Chinese Academy of Sciences, Beijing, China (Y. Wang, Liu, Zhong, and Wan); the Graduate University of Chinese Academy of Sciences, Beijing, China (Y. Wang); the College of Chemistry and Life Sciences, Zhejiang Normal University, Jinhua, Zhejiang, China (Y. Wang); and the Department of Wildlife, Fisheries and Aquaculture, Mississippi State University, Mississippi State, MS 39762 (G.M. Wang).

Address correspondence to G.M. Wang at the address above, or e-mail: gwang@cfr.msstate.edu.

Abstract

Social behavior can shape the local population genetic structure of mammals. Group living can increase pairwise genetic relatedness of mammals at a local level but differentiate the genetic structure at a population level through offspring philopatry and nonrandom mating. Our study aimed to test the hypothesis that social groups of Mongolian gerbils (*Meriones unguiculatus*) would consist of genetically related individuals due to offspring philopatry and would have distinct genetic structures because of restricted gene flow among social groups and nonrandom mating. We genotyped 327 wild gerbils, live captured from 28 social groups in Inner Mongolia, China, using nine microsatellite loci. The within-group pairwise genetic relatedness coefficient averaged 0.28 ± 0.14 (standard deviation), whereas the average pairwise genetic relatedness coefficient of the whole gerbil population was 0.0 ± 0.2. Additionally, the value of the global F statistic (F_{st}) was 0.21, suggesting a substantial genetic differentiation among social groups of Mongolian gerbils. The Bayesian clustering divided the 327 gerbils into 23 distinct genetic clusters. Therefore, our results show that high within-group genetic relatedness and among-group genetic differentiation are the genetic consequences of group living in social mammals because of restricted gene flow, female philopatry, and nonrandom mating within social groups.

Key words: Meriones unguiculatus, *microsatellite, Mongolian gerbils, population genetic differentiation, social groups*

Group living occurs in diverse taxa of animals, including insects, fish, birds, and mammals (Krause and Ruxton 2002). However, the evolutionary causes of group living are still controversial (Kokko 2007; Lacey and Sherman 2007; Clutton-Brock 2009). Evolutionary theory posits that social groups evolve when direct and indirect fitness benefits of group living exceed the fitness costs of group living or the fitness benefits of living alone (Emlen 1994). Reciprocity or mutualism can maintain cooperative breeding among non-kin in vertebrate societies when direct benefits of group living outweigh costs of living together (Clutton-Brock 2002, 2009; Fletcher et al. 2006; Bergmuller et al. 2007; Kokko 2007). However, some offspring that remain at their natal sites may not reproduce in the presence of breeding parents or siblings and thus do not gain any direct fitness benefits (Emlen et al. 1998). Nonbreeding offspring may help feed and protect the offspring of breeding kin to gain indirect fitness benefits (i.e., alloparental care or altruism; Emlen 1994; Solomon and Getz 1997). Group living or altruism evolves when indirect benefits outweigh costs; thus, kin selection offers a potential explanation of the evolution of group living (Hamilton 1964).

Understanding the genetic structure of social groups is important to understand the evolution and maintenance of group living (Dobson 2007). Philopatry of offspring may increase within-group genetic relatedness (or kinship) of group mammals (Chesser 1991a). Within-group genetic relatedness may make group mates amicable and tolerable to each other and may reduce within-group competition (Ylonen et al. 1990; Silk 2007). Furthermore, altruistic offspring may gain indirect fitness benefits through alloparental care and kinship with breeding individuals. It is unlikely that kin selection operates or is a main evolutionary force in group-living mammals if within-group genetic relatedness is less than the expected mean genetic relatedness between 2 randomly selected individuals.

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Therefore, greater-than-average genetic relatedness between group mates is a prerequisite of kin selection (Chesser 1991a).

Social behavior influences local population genetic subdivisions of group-living mammals (Chesser et al. 1993; Storz 1999). At the level of the local population, the philopatry and maternal coancestry of group mates can subdivide the population genetic structure of mammals due to nonrandom mating and limited gene flow between social groups (Chesser 1991b; Dobson 2007). If territoriality or social barrier is sufficient to restrict gene flow between social groups, genetic drift, occurring in social groups due to random sampling of alleles, may diversify among-group genetic structure (Storz 1999). The subdivision of genetic structure among adjacent social groups may be maximized by female philopatry and the mating monopoly of the plural breeding females of a social group by a single male, resulting in a significant fraction of between-group genetic variance and high within-group genetic relatedness (Storz 1999). Therefore, it is plausible to hypothesize that there exists significant between-group genetic variation in group-living mammals as a consequence of group living.

The Mongolian gerbil (*Meriones unguiculatus*) is a social rodent distributed throughout the desert grassland and agricultural land of Inner Mongolia in China, Mongolia, and Russia (Liu et al. 2007). Social behavior of Mongolian gerbils has been well studied in laboratory or seminatural conditions (Agren et al. 1989a, 1989b; Clark and Galef 2001; Scheibler et al. 2004). Mongolian gerbils exhibit strong but variable sociality, living in groups year-round with social group sizes ranging from 2 to 18 individuals (Agren et al. 1989a; Liu, Wang, Wang et al. 2009). A social group consists of a breeding pair and its offspring, particularly female offspring (Agren et al. 1989a; Liu, Wang, Wang et al. 2009). Mongolian gerbils are socially monogamous. In laboratory or enclosure studies, male and female founders form a pair bond and are the only breeding individuals of a social group until one of them dies or disappears (Agren 1984; Clark and Galef 2001; Scheibler et al. 2004). However, recent field studies have found extrapair mating (Agren et al. 1989a, 1989b) and multiple breeding females in a social group of wild Mongolian gerbils (Liu, Wang, Wang et al. 2009). Moreover, female offspring of gerbils are philopatric, particularly at a high density (Liu, Wang, Wang et al. 2009). Although these characteristics suggest that genetic variability within social groups should be lower than that between groups, genetic consequences of group living have not been quantified with genetic methods in Mongolian gerbils. The objectives of our study were to 1) estimate pairwise genetic relatedness between group mates and test the hypothesis that social groups of Mongolian gerbils would consist of highly genetically related individuals due to philopatry of offspring and 2) estimate the genetic differentiation of the gerbil population studied and test the hypothesis that social groups of Mongolian gerbils have distinct genetic structures owing to philopatry of offspring and nonrandom mating.

Materials and Methods

Study Site

Our study was conducted at Xima Gou (village; lat 115°22′E, long 42°07′N, 1450 m elevation), about 30 km north of Baochang, Taipusi Qi (county), Inner Mongolia, China. The area was in a typical region where steppes were intermixed with cropland. The climate was semiarid, with a relatively hot summer and a cold dry winter. Average monthly temperatures ranged from −19.1 to 21.1 °C. Average annual total precipitation was about 350 mm, ranging from 258 to 550 mm. Snow cover lasted about 90 days from mid- or late October to early April (Liu et al. 2007).

Our trapping plot was situated on a 9-ha grassland (300 × 300 m) surrounded by wheat (*Triticum* spp.) and cabbage (*Brassica* spp.) cropland. The vegetation was dominated by the grass *Leymus chinensis* and the herb *Corispermum mongolicum*. Moreover, it consisted of a mixture of grasses such as *Cleistogenes squarrosa* and *Setaria viridis*; herbs including *Artemisia sieversiama*, *A. scoparia*, and *Heteropappus altaicus*; and small shrubs *Caragana microphylla* and *C. korshinskii*. The nearest neighboring gerbil population was about 1.5 km from our study site. No livestock grazed at the study site during our study.

Capture–Recapture Methods

Mongolian gerbils were live trapped from 28 April to 21 October in 2006 at 2-week intervals. To enhance the probability of captures, we used a concentric circle trapping method (Liu et al. 2007). Trap stations were arranged in 3–4 concentric circles at equal spacing at each burrow system. Four to 16 trap stations were spaced equally on each circle. One wire-mesh live trap (28 × 13 × 10 cm) was placed at each station with the trap door opening facing a burrow entrance or gerbil runway (Liu et al. 2007). About 450 traps were placed at all the entrances of each burrow system each week. Traps were baited with fresh peanuts at the time of trapping. Each trapping period lasted for 3 consecutive days. Details of our trapping methods and procedures can be found in Liu, Wang, Wang et al. (2009).

All captured gerbils were toe clipped at the first capture for permanent identification (ID). The clipped toes were preserved in 75% ethanol for microsatellite DNA analysis. Captured gerbils were sexed and weighed to the nearest 0.1 g. Reproductive condition, trap location, and ID number were recorded for each capture. Males were considered in reproductive condition if they had scrotal testes and visible ventral scent glands with either clear contour or large visible pores surrounded by secreted substance. Female gerbils were considered in reproductive condition if they had a bulging abdomen, enlarged nipples surrounded by white mammary tissue, or opened pubic symphysis (Liu et al. 2007). We classified Mongolian gerbils as juveniles if weighing less than 30 g, subadults if weighing between 30 and 50 g, and adults if weighing more than 50 g. Captured animals were released at the

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site of capture. We considered gerbils captured in the same burrow system in 2 consecutive trapping sessions to be members of the same social group (Agren et al. 1989). Our trapping and handling of Mongolian gerbils followed the guidelines of Animal Care and Use Committee of the American Society of Mammalogists (Gannon et al. 2007) and was approved by the Institutional Animal Use and Care Committee of the Institute of Zoology, Chinese Academy of Sciences.

Microsatellite Analysis

DNA was extracted from the toe tissues of gerbils using phenol–chloroform extraction methods after Sambrook and Russell (2001). The quality and quantity of extracted DNA were visually examined on agarose gels stained with ethidium bromide. Nine microsatellite markers *Mungμ1*, *Mungμ2*, *Mungμ3*, *Mungμ4*, *Mungμ5*, *Mungμ6*, *Mungμ7*, *Mungμ8*, and *Mungμ9*, which were developed for Mongolian gerbils (Neumann et al. 2001), were used to genotype the members of the study population. Polymerase chain reactions (PCRs) were carried out in a 10 μl reaction volume containing approximately 50 ng genomic DNA, 5 μl Premix Taq (TaKaRa Bio Company, Madison, WI), and 0.6 μM of forward (fluorescently labeled with 5′-TAMARA, HEX, or FAM) and reverse primers. The PCR protocol was as follows: initial denaturation at 95 °C for 5 min, 30 cycles of denaturation at 94 °C for 40 sec, annealing at the temperature (T_a) for 45 s, extension at 72 °C for 1 min, and a final extension step at 72 °C for 7 min. The specific annealing temperature (T_a) for each marker was specified in Neumann et al. (2001). Amplified fragments were electrophoresed on an ABI PRISM 377 automated sequencer (Applied Biosystems, Foster City, CA) and analyzed using Genescan Version 3.7 (Applied Biosystems). Each gerbil sample was genotyped independently by 2 different observers to assess typing error rates. If the genotypes of a gerbil from 2 observers differed, genotyping was repeated until a consensus was reached.

Statistical Analyses

We tested for the presence of null alleles, short allele dominance, and typing error associated with stutter using the program MICRO-CHECKER (Van Oosterhout et al. 2004). A simulation study showed that the presence of null alleles in a frequency of less than 0.2 does not cause any significant bias or error in parentage analysis (Dakin and Avise 2004). Therefore, we included microsatellite loci, which had null allele frequencies of less than 0.1, in our analysis. We tested the Hardy–Weinberg equilibrium (HWE) at each locus and linkage disequilibrium (LD) between each pair of loci in the subpopulation of 67 adults that weighed more than 50 g at their initial captures, using the program GENEPOP 3.4 with the Markov chain option of 50 batches and 100 000 iterations per batch (Raymond and Rousset 1995). The HWE at each locus and LD also were tested by social groups. We carried out separate tests for each social group that had more than 10 individuals, whereas we combined data on the social groups that were of less than 10 individuals into one group for the HWE and LD tests. If a locus is significant in the HWE test for the combined group, we concluded that the departure from the HWE at the locus was probably due to the Wahlund effects (Freeland 2005). Additionally, inconsistent results of the LD tests for the same pair loci across social groups also provide evidence that the pair of loci is not physically linked (or located on the same chromosome; Gauffre et al. 2008). We used Bonferroni correction for multiple comparisons with a nominal significance level of 0.05. We also calculated mean numbers of alleles per locus, allele frequencies, observed and expected heterozygosities at each locus, and Wright's F statistic (F_{st}) and inbreeding coefficient (F_{is}) using the program GENALEX 6.4 (Peakall and Smouse 2006). Inbreeding coefficients (F_{is}) were calculated for each group as well.

We calculated average pairwise within-group genetic relatedness coefficients using GENALEX. We chose the bootstrap option to calculate mean Queller and Goodnight relatedness coefficients (Queller and Goodnight 1989) and 95% confidence intervals (CI) with 1000 iterations. The bootstrap procedure resamples allele frequencies based on observed allele frequencies at each locus (Peakall and Smouse 2006). We used paired t-tests to detect differences in mean within-group pairwise genetic relatedness between the sexes over 26 social groups. We also compared means of observed and expected heterozygosities of the 7 loci using paired t-tests. The significance level of the tests was set to 0.05. Means were reported ± standard deviation.

We used Bayesian clustering analysis within the program STRUCTURE 2.3 to estimate the number of genetic clusters (K) without any prior population information (Pritchard et al. 2000). We carried out 5 independent runs of STRUCTURE for each of $K = 1$–29. Each run had 100 000 iterations for Bayesian inferences, following a burn-in period of 100 000 iterations. We assumed the admixture model, which allows a mixture of genetic ancestries for an individual, with the option of allele frequencies being not correlated. We determined the most likely number of genetic clusters K using the ΔK method (Evanno et al. 2005). The Bayesian clustering aimed to demonstrate the distinct genetic structure of social groups but not at the population level.

We used the program FSTAT to detect male-biased dispersal in juvenile gerbils with 10 000 iterations (Goudet 1995). We used one-sided tests to test the null hypothesis that male-biased dispersal results in greater mean genetic relatedness and greater mean value of corrected assignment index (AIc) in the subpopulation of female juveniles than in the subpopulation of male juveniles. We set the significance level of the tests to 0.05. We also reconstructed the full- and half-sibship from 260 juvenile and subadult gerbils genotyped using the program COLONY 2.2 (Jones and Wang 2010), with the dropout rate of 0.0, typing error rate of 0.0001, and the assumption of monogamous mating for females. We used all adult

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Table 1 Numbers of alleles per locus (N_a), observed heterozygocity (H_o), and expected heterozygocity (H_e) of Mongolian gerbils genotyped using microsatellite loci in Inner Mongolia, China

Locus	N	N_a	H_o	H_e
Mungμ1	327	17	0.91	0.89
Mungμ2	327	18	0.80	0.87
Mungμ3	327	13	0.77	0.84
Mungμ4	327	18	0.80	0.85
Mungμ5	327	19	0.82	0.86
Mungμ6	327	19	0.74	0.81
Mungμ7	327	20	0.87	0.87

females as at their initial captures and breeding subadult females captured before the initial captures of juveniles and subadults as candidate mothers but did not assume any known maternity. Sibship and maternity were determined with a probability of 0.8 or greater.

Results

We genotyped a total of 327 gerbils from 28 burrow systems. More than 80% of burrow entrances were located within 6 m from the center of a burrow system. The distance between 2 burrow systems ranged from 15.8 to 274.9 m with an average of 123 ± 58.7 m. Therefore, burrow systems were separated spatially, with no or few burrow entrances found between 2 burrow systems. During 2 successive trapping weeks, social group size ranged from 2 to 18 individuals and averaged about 7.0 ± 3.84 individuals, consisting of 0–4 breeding males, 0–3 breeding females, and 0–11 juveniles. Sex ratios (proportions of females) of social groups ranged from 0.00 to 1.00 and averaged 0.60 ± 0.26.

MICRO-CHECKER did not detect either small allele dominance or scoring error caused by stutter at any of the 9 loci. No null alleles were found at the loci *Mungμ1* and *Mungμ9*. Null allele frequencies of the loci *Mungμ2–Mungμ7* were less than 0.05, whereas that of *Mungμ8* was 0.32. Substantial missing data existed at *Mungμ9* due to allele scoring difficulties. Therefore, we excluded *Mungμ8 and Mungμ9* from further analysis. Only locus *Mungμ1* significantly departed from the HWE ($P = 0.002$) in the adult subpopulation of 67 gerbils. Only *Mungμ2–Mungμ3* pair was in the LD ($P = 0.001$) in the adult subpopulation. Thirteen social groups had more than 10 gerbils. All 7 loci were in the HWE in 11 of the 13 social groups; one group had only *Mungμ3* in departure from the HWE ($P = 0.005$); and the remaining group had *Mungμ5–7* in departure from the HWE ($P = 0.0$, 0.001, and 0.004). In the combined group, only *Mungμ1*, *3*, and *6* were in the HWE, whereas the remaining loci departed from the HWE probably due to the Wahlund effects. All 21 possible pairs of the 7 loci were in the linkage equilibrium in 9 social groups; 4 groups had 1, 2, 2, and 9 pairs of loci in the LD, respectively. However, none of these pairs was consistently in the LD in the 4 social groups. Furthermore, the results of the HWE and LD tests were inconsistent between the adult subpopulation and social groups, suggesting that the inclusion of multiple siblings may be a reason of the departure from the HWE in the combined group.

Numbers of alleles per locus ranged from 13 to 20, and observed heterozygosity ranged from 0.8 to 0.91 (Table 1). Mean observed heterozygosity over the 7 loci (mean H_o = 0.82) was significantly lower than that of expected heterozygosity (mean H_e = 0.88; P = 0.02). The probability of exclusion with all 7 loci combined was 1.0, and the probability of identity was 7.9×10^{-11}. We did not estimate mean within-group pairwise genetic relatedness for 2 social groups that had only 2 gerbils each; thus, only data from animals resident in 26 social groups over the entire study period were included in analyses of within-group pairwise relatedness. The bootstrap values of within-group pairwise genetic relatedness coefficients averaged 0.28 ± 0.14 (95% CI: 0.23–0.34) over the 26 social groups, whereas the average pairwise genetic relatedness coefficient of the whole gerbil population was 0.0 ± 0.2 (95% CI: −0.002 to 0.002). Five social groups had mean pairwise relatedness coefficients of less than 0.1, whereas the remaining 21 groups had mean pairwise relatedness coefficients of greater than or equal to 0.15 (Figure 1). The mean within-group pairwise relatedness of male group mates averaged 0.26 ± 0.15, whereas that of female group mates averaged 0.32 ± 0.16. However, mean within-group pairwise relatedness coefficients did not differ between the sexes (paired t =1.74, P = 0.08, degrees of freedom = 18).

We identified 48 pairs of males and females that were reproductively active in 17 social groups during the same trapping period, suggesting more than one breeding pair per social group (2.8 ± 2.2 breeding pairs per group). We did not find breeding pairs in the remaining 9 social groups. Genetic relatedness between the male and female in a breeding pair averaged 0.08 ± 0.26 (95% CI: 0.007–0.15).

The population-level F_{st} value was 0.2, and the F_{is} value was −0.2. Group-specific F_{is} ranged from −0.01 to −0.45 (Appendix Tables A1 and A2). Furthermore, the ΔK value of the STRUCTURE run assuming 23 genetic clusters was 52.3, whereas the second highest ΔK value was 31.7 for K = 17. Therefore, STRUCTURE classified the 327 gerbils into 23 distinct genetic clusters (Figure 2). The mean assignment index (AIc) of male juveniles was −0.43, significantly lower than that of female juveniles (AIc = 0.39; P = 0.049). Mean genetic relatedness of the subpopulation of male juveniles (mean4 r = 0.20) was significantly lower than that of the subpopulation of female juveniles (mean r = 0.28; P = 0.008).

We identified 63 full-sib clusters, with 2 or more full siblings each cluster. Of the 63 full-sib clusters, 53 clusters also had one or more half-sibling identified. We also

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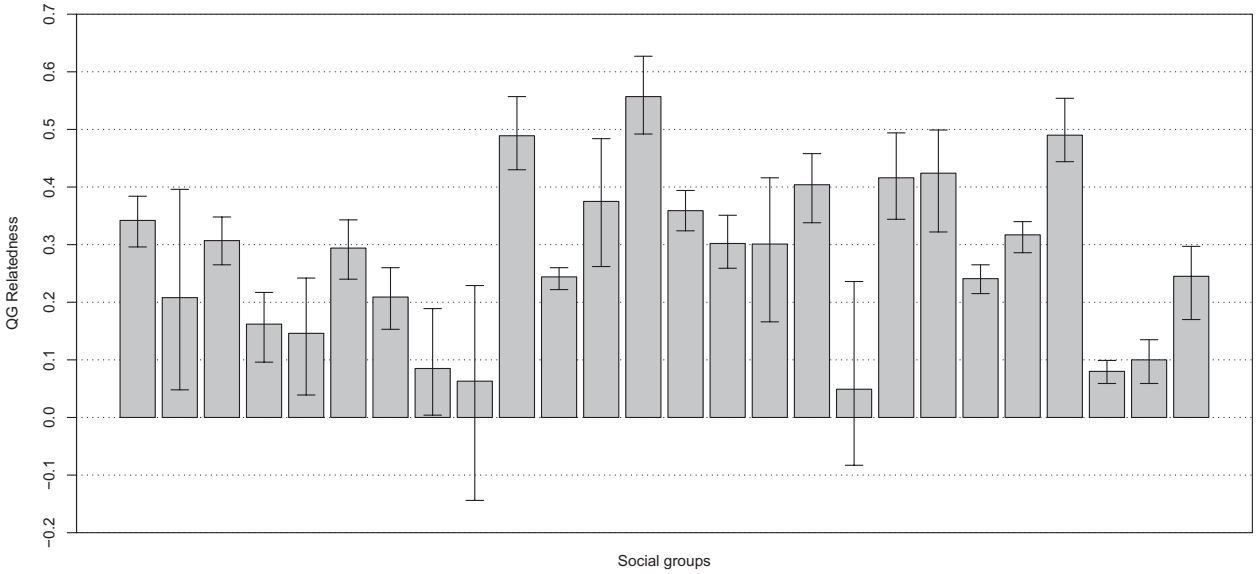

Figure 1. Bootstrap mean within-group Queller and Goodnight genetic relatedness coefficients and 95% CI of Mongolian gerbils genotyped with 7 microsatellite loci in Inner Mongolia, China. Vertical lines are 95% CI.

identified 30 maternally half-sib clusters, of which each had 2 or more half siblings assigned to the same maternity. We captured all members of each of the 75 full- or half-sib clusters at the same burrow system. Some members of each of the 50 sibling clusters were captured together with their mothers at the same burrow system for 2 (a month) to 7 trapping periods (3.5 months). For example, male offspring gtwo340 of female gtwo320 was captured together with its female full siblings gtwo330, gtwo340, and gtwo420 for 3 months at the burrow system gtwo.

Discussion

Group members of Mongolian gerbils were highly genetically related. Within-group pairwise genetic relatedness coefficient averaged 0.28 over all social groups genotyped, with the 95% CI ranging from 0.23 to 0.34, indicating either first or second order kinship. Our sibship analyses and live trapping data suggest that some full- and half siblings, including males, lived with mothers up to 7 trapping periods (3.5 months). The average lifespan of wild Mongolian gerbils is about 5 months (Liu, Wang, Wang et al. 2009). Thus, offspring, particularly female offspring, of female gerbils delayed their dispersal. This finding is consistent with data on the demography of Mongolian gerbils from a separate study. Fifty percent or more offspring of Mongolian gerbils were philopatric (Liu, Wang, Wan et al. 2009). The philopatry of genotyped gerbil offspring might mechanistically increase within-group pairwise genetic relatedness. A long-term monitoring and DNA analysis demonstrated that the females of great gerbils (*Rhombomys opimus*) are philopatric and genetically related (Randall et al. 2005). High within-group genetic relatedness has also been observed in other group-living

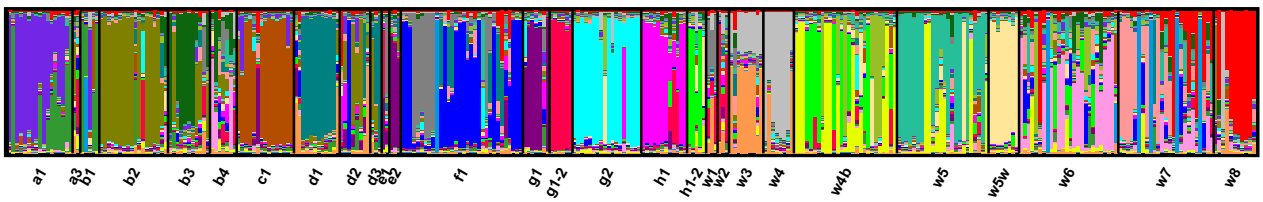

Figure 2. Bayesian genetic clustering of Mongolian gerbils in Inner Mongolia, China, using 7 microsatellite loci and the program STRUCTURE. Symbols below the figure are labels of social groups; vertical black lines are the separators between social groups; and colors represent genetic clusters.

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mammals, such as North American beavers (*Castor canadensis*) and black-tailed prairie dogs (*Cynomys ludovicianus*) (Manno et al. 2007; Crawford et al. 2008). Therefore, marked within-group pairwise genetic relatedness in our study population is likely a genetic consequence of group living.

Theory suggests that group living, polygyny, and philopatry of offspring should result in the local genetic subdivision of populations of group-living mammals (Chesser 1991a, 1991b; Dobson 2007). Nonrandom mating, restricted gene flow, and genetic drift result in genetically heterogeneous matrilineal groups. However, empirical data were dubious with the role of social structure in the population genetic subdivision of social mammals. Storz (1999) compiled genetic data on 18 species of social mammals but found that majority of species had the F_{st} value of less than 0.05 except for black-tailed prairie dogs, red howler monkeys (*Alouatta seniculus*), and white-tailed deer (*Odocoileus virginianus*). Our study provides further empirical evidence for the role of group living in subdividing population genetic structure of social rodents. The population genetic structure of Mongolian gerbils on our site was subdivided with an F_{st} value of 0.2, which indicates moderate genetic differentiation among social groups (Storz 1999; Freeland 2005). Likewise, the F_{st} value of group-living black-tailed prairie dogs in New Mexico is 0.23 and 0.17 in South Dakota (Storz 1999). Furthermore, in spite of the mixed ancestry of some individuals, most of the gerbil social groups had distinct genetic structures (Figure 2). Mongolian gerbils are territorial and defend territories collectively (Agren et al. 1989a, 1989b). Social barriers/fences may limit natal dispersal of female offspring and gene flow between social groups and subsequently result in genetic differentiation among social groups (Storz 1999; Dobson 2007).

Sex-biased gene flow, female philopatry, and nonrandom mating in group-living mammals may result in excessive genetic heterogeneity within social groups or matrilineal groups, with negative F_{is} values (Storz 1999). The value of the inbreeding coefficient (F_{is}) was −0.2 in Mongolian gerbils, suggesting that within-group heterogeneity is greater than expected under the HWE, possibly owing to male-biased dispersal of juveniles. The average genetic relatedness of the subpopulation of juvenile females was 1.23 times higher than that of the subpopulation of juvenile males ($P = 0.008$). Although our sibship and maternity analyses suggested that some male offspring delayed dispersal, a juvenile male was more likely to be an immigrant than was a juvenile female, with a negative mean AIc index. Additionally, sex ratios of our gerbil population were female biased (Liu, Wang, Wang et al. 2009). Therefore, male offspring of Mongolian gerbils may disperse to mate with unrelated females in nonnatal social groups to avoid inbreeding. The average pairwise genetic relatedness coefficient of breeding pairs on our study site was 0.08 (95% CI: 0.007–0.15), suggesting a relatively low level of inbreeding. In free-living populations of Mongolian gerbils, social organization and natal dispersal may mechanistically maintain high genetic diversity.

The Mongolian gerbil is a popular animal model in biomedical and behavioral studies (Razzoli et al. 2003). Laboratory colonies for scientific research all over the world were developed from 20 pairs imported from Japan in 1954, which descended from the gerbils originally captured in eastern Mongolia in the 1930s. Inbreeding has resulted in a significant loss of genetic diversity, with the average percentage of polymorphic amplified fragment length polymorphism loci being 7.5% in North American colonies (Razzoli et al. 2003). Microsatellite loci *Mungμ1*, *2*, *3*, and *9* were monomorphic; observed heterozygosities of *Mungμ4*, *5*, *6*, *7*, and *8* ranged from 0.022 to 0.467 in captive gerbils from European colonies (Neumann et al. 2001). Likewise, observed heterozygosities at the same microsatellite loci of laboratory gerbils from a 20-generation laboratory colony in Zhejiang, China ranged from 0 to 0.72 and averaged 0.47 (Liu et al. 2005). However, observed heterozygosities at the loci *Mungμ1–7* of wild Mongolian gerbils in the Republic of Mongolia were similar to those in Inner Mongolia, China, ranging from 0.7 to 0.88 (Neumann et al. 2001).

Studies of the effects of within-group pairwise genetic relatedness on the lifetime reproductive output or individual fitness of group-living animals are critical to understand the evolution of group living (Lacey 2004; Lacey and Sherman 2007). Although group mates of Mongolian gerbils are highly genetically related, little is known about demographic effects of genetic relatedness in Mongolian gerbils. Our trapping data did not have sufficient temporal resolutions needed for complete genetic parentage analysis. Therefore, genetic analyses of the offspring parentage, lifetime breeding success, and genetic relatedness of Mongolian gerbils are needed in the future studies to better understand kin selection and the evolution of group living in Mongolian gerbils.

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Appendix

Table A1 Sample size (n) and Wright's inbreeding coefficient (F_{is}) of Mongolian gerbils captured at burrow systems 1–14

Burrow system	1	2	3	4	5	6	7	8	9	10	11	12	13	14
n	17	5	18	7	15	12	8	2	32	6	7	5	2	3
F_{is}	−0.18	0.09	−0.15	−0.20	−0.22	−0.18	−0.07	−0.62	−0.09	−0.44	−0.25	−0.19	−0.14	−0.20

Table A2 Sample size (n) and Wright's inbreeding coefficient (F_{is}) of Mongolian gerbils captured at burrow systems 15–28

Burrow system	15	16	17	18	19	20	21	22	23	24	25	26	27	28
n	3	3	3	9	8	27	24	8	26	25	11	18	11	12
F_{is}	−0.45	−0.41	−0.24	−0.13	−0.27	−0.06	−0.11	−0.40	−0.07	−0.01	−0.20	−0.23	−0.14	−0.21

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